

Reproductive Potential of Overwintering, F₁, and F₂ Female Boll Weevils (Coleoptera: Curculionidae) in the Lower Rio Grande Valley of Texas

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ABSTRACT The feeding and oviposition activity of overwintering boll weevils, *Anthonomus grandis grandis* (Boheman), and seasonal fluctuations in development, survival, and reproduction of progeny of overwintering and first- and second-generation boll weevil females were determined in the laboratory at 27°C, 65% RH, and a photoperiod of 12:12 (L:D) h. During the cotton-free period in the Lower Rio Grande Valley, female boll weevils without access to cotton resorb their unlaid eggs and enter reproductive diapause. However, when they were provided daily with greenhouse-grown cotton squares, commencement of oviposition began after 7, 15, or 20 d, depending on when they were captured. Females captured later in the winter fed longer before laying eggs than those captured in the early fall, suggesting that it may take females longer to terminate diapause the longer they have been dormant. The rate of feeding by females was significantly less during the winter months, and this may have affected the rate of diet-mediated termination of dormancy. Females of the first and second generations after the overwintering generation produced a significantly higher percentage of progeny surviving to adulthood and a higher proportion of these progeny were females. Offspring development time from overwintering female parents was significantly longer than that from first and second generations under the same laboratory conditions. The total number of lifetime eggs produced by females of the second generation during the cotton-growing season were \approx 9.9-fold higher than for overwintering females and 1.5-fold higher than for first-generation females. Life table calculations indicated that the population of second-generation boll weevils increased an average of 1.5-fold higher each generation than for females of the first generation and 22.6-fold higher than for overwintering females. Our data showed variation in boll weevil survival, development, and reproductive potential among the overwintering and first- and second-generation females, suggesting inherent seasonal fluctuations in these parameters.

KEY WORDS *Anthonomus grandis grandis*, survival, development, reproduction, seasonal variation

The boll weevil, *Anthonomus grandis grandis* (Boheman), is a key pest of cotton in noneradication areas of the United States, Mexico, and South America. The adult boll weevil has a prolonged snout with chewing mouthparts at the tip. It ranges from 3.2 to 8 mm in size and from reddish brown to dark gray in color. Female weevils oviposit eggs in squares and young bolls. The larva is a legless white grub that develops through three instars and a pupal stage. All development from egg to adult occurs inside the fruit and requires 15–20 d. Adults cause damage through feeding and oviposi-

tion punctures on fruiting structures, whereas larvae feed within the fruit. Bracts on damaged squares open, which is referred to as flaring, and damaged squares usually abscise from the plant.

The seasonal reproductive potential of boll weevil populations is an important consideration in determining the success of any control strategy. Basic research designed to address unanswered questions on the seasonal dynamics of boll weevils is vital to successful expansion of eradication, containment, and management programs into subtropical and tropical environments. In the subtropical Lower Rio Grande Valley (LRGV) of Texas, reproduction is halted in diapausing adults, and metabolic activity is suppressed (Wolfenbarger et al. 1976, Graham et al. 1978, 1979, Guerra et al. 1982, Summy et al. 1993). In the subtropics and tropics, diapause functions to help the boll weevil survive periods of food shortage while permitting activity during extended periods of relatively mild climatic conditions (Guerra et al. 1984, Summy et al. 1988). Diapause is terminated when squares become available for feeding and ovipositing regardless of the

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season (Spurgeon and Suh 2003, Spurgeon et al. 2003). The survival and reproductive rates of first- and second-generation boll weevils during the cotton growing season are strongly dependent on the fruiting characteristics of cotton plants (Greenberg et al. 2003, 2004, 2005). However, the controlling factors of boll weevil population dynamics during the year have not been extensively studied. Additional clarification of boll weevil mortality and reproduction may reveal opportunities for improved effectiveness of strategies for suppression and eradication of populations.

The objectives of this study were to examine seasonal fluctuations in oviposition and in survival of progeny of overwintering and first- and second-generation female boll weevils under controlled conditions.

Materials and Methods

Boll Weevil Culture and Cotton Squares. The study was conducted in Hidalgo County, TX (2000–2005). Overwintering boll weevils were collected from pheromone traps once every 10 d from September to March and evaluated for survival. Twenty traps were placed around the perimeter of experimental plots at the North Farm and 10 around plots at the South Farm of the Subtropical Agricultural Research Center, where cotton had been planted in previous years and had a history of boll weevil infestations. The weevils were taken to the laboratory, where the numbers of boll weevils were recorded. Weevils collected in a single day at intervals from the second week of September to March (100–150/mo) were used to evaluate feeding and oviposition activity of overwintering boll weevils. The sex of each collected overwintering weevil was determined using the method of Sappington and Spurgeon (2000). Mixed-sex groups of five females and five males were held in 15-cm-diameter petri dishes ventilated by a 4-cm-diameter screened hole in the lid. Petri dishes were placed in an environmental chamber maintained at $27 \pm 1^\circ\text{C}$, 65% RH, and a photoperiod of 12:12 (L:D) h. Temperature and relative humidity were monitored by a Fisher-brand Traceable Relative Humidity Meter with temperature readout (Fisher cat. no. 11-661-12; Control Co., Friendswood, TX). Each dish contained a cotton wick saturated with water and was provided daily with 10 greenhouse-grown squares that were 7–10 mm diameter at the widest part of the flower bud with intact bract. For the seasonal fluctuation in development, survival, and reproduction of progeny of overwintering and first- and second-generation boll weevil females (second set of experiment), we used for overwintering weevils, those which were trapped in February (≈ 150 weevils), and for first and second generations, weevils were reared from field-collected squares infested with third instars in May–June ($\approx 1,000$) on growing cotton. Infested squares with third instars were held in screen cages (20 by 20 by 20 cm) in an environmental chamber with the conditions describe above until completion of larval development. Pupae were harvested from squares and placed

in petri dishes containing a thin layer of moist vermiculite. Pupae were examined daily until adult eclosion. On the day of eclosion, the sex of each adult was determined. Mating of the weevils (groups of five males and five females) was facilitated by a 5-d conditioning period using the same environmental conditions that were used for rearing adults.

Experimental Design and Procedure. For the first set of experiments, we took a monthly random sample of 15 females. Each female was isolated in a petri dish and provided with five uninfested greenhouse-grown squares, which were replaced daily for the first 10 d after onset of oviposition. After removing the squares, both feeding punctures (open) and oviposition punctures (sealed) were counted. Oviposition punctures were distinguished by a frass plug and/or a waxy substance either closing the puncture or present on the periphery of the puncture. We used the numbers of sealed punctures as a relative estimate of egg numbers based on the report of Everett and Ray (1962) of a strong correlation between the numbers of sealed punctures and the number of eggs that a boll weevil deposits. The total number of punctures in each square was used as a measure of boll weevil puncturing activity, whereas the ratio of sealed punctures to total punctures was used to characterize oviposition activity (Everett and Earle 1964).

For the second set of experiments, 20 randomly selected females for each treatment (overwintering and first- and second-generation weevils) were held individually in a petri dish and provided with five fresh squares daily under the conditions described above until weevil death. Squares were removed and checked for feeding and oviposition punctures.

In addition to monitoring feeding and oviposition, the percentage of eggs that ultimately produced an adult, development time, and the sex ratio of adult progeny were estimated from cohorts of squares periodically obtained from each treatment. To avoid underestimating the production of adults because of larval cannibalism, only squares containing a single egg puncture were selected. The number of egg-punctured squares comprising each cohort varied based on their availability. Each cohort was held in a vented petri dish. Square-reared cohorts were maintained under the same environmental conditions as adults. Plates were observed daily for newly emerged adults beginning on day 12 and until day 20 after oviposition. After day 20, squares were opened to determine if additional live weevils remained.

For reproductive capacity, presence of oocytes, oocytes with yolk, and chorionated eggs of 28 females trapped monthly (September through March and June) were determined under a dissecting microscope using the method of Spurgeon et al. (2003).

Statistical Analyses. Data for feeding and oviposition activity of overwintering weevils during September to February (feeding and egg punctures, ratio of egg punctures to total, and percentage of squares attacked per female per day) and data to test seasonal variations of overwintering and first- and second-generation boll weevil females (lifetime oviposition, total

Table 1. Feeding and oviposition activity of overwintering boll weevils

Month	Punctures/female/d				Percentage of squares attacked
	Feeding	Egg	Feeding + egg	Puncture ratio	
Sept.	10.2 ± 0.7a	9.6 ± 0.7a	19.8 ± 1.2a	0.403 ± 0.02a	79.4 ± 2.8a
Oct.	12.4 ± 1.2a	7.1 ± 0.6b	19.5 ± 1.4a	0.385 ± 0.03a	82.0 ± 2.8a
Nov.	9.8 ± 0.7a	3.4 ± 0.4c	13.2 ± 0.8b	0.263 ± 0.03b	51.2 ± 5.4c
Dec.	7.5 ± 0.8ab	2.8 ± 0.5c	10.3 ± 0.9bc	0.273 ± 0.04b	65.2 ± 3.3b
Jan.	5.5 ± 0.4b	1.5 ± 0.2cd	7.0 ± 0.5cd	0.168 ± 0.02b	48.1 ± 3.1c
Feb.	4.1 ± 0.4b	0.4 ± 0.1d	4.5 ± 0.4d	0.079 ± 0.02c	29.0 ± 1.9d

Means ± SE within a column followed by the same letter are not significantly different (Tukey-Kramer test, $P < 0.05$).

development time of progeny, percentage of emergence, and percentage of progeny that were female) were examined by one-way analyses of variance (ANOVA) using PROC GLM (SAS Institute 1999). When significant F -values were obtained, means were separated using the Tukey-Kramer test (TUKEY option of the LSMEANS statement; SAS Institute 1999). Percentage data were analyzed as arcsine-square root transformed proportions (Sokal and Rohlf 1995), but results are presented as untransformed means.

The numbers of oviposition punctures observed for each weevil each day in the overwintering and first and second generations were examined by repeated-measures ANOVA (PROC MIXED; Littell et al. 1996). The model used a compound symmetry covariance structure and contained terms for time (day), seasonal development, and their interaction. Homogeneity of female survival curves among seasonal development was tested with the LIFETEST procedure of SAS (SAS Institute 1999). A closed testing procedure (Hommel 1988) was used to determine if survival curves for overwintering and first and second generations could be distinguished.

An estimate of boll weevil population growth rate was obtained for females corresponding to each season of development by calculating life table statistics. For each treatment, the jackknife program of Hulting et al. (1990) was used to calculate the net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), the finite capacity of increase (λ , defined as the number of times a population multiplies itself per unit of time), the mean generation time (T), the doubling time (DT) of the population, and the total progeny produced per female. The growth index (GI) was calculated by dividing the percentage survival of immatures by development time (Setamou et al. 1999).

Results

Overwintering Boll Weevil Characterization

Our data showed a reduction in numbers of trapped weevils over the winter in the LRGV, likely related to boll weevil mortality. The number of captured boll weevils per trap decreased during the cotton-free period from September through March (i.e., from post-harvest to early spring) by 6.3-fold (from 21.5 ± 5.4 to 3.4 ± 0.3) during 2000–2001, by 5.3-fold (from 39.1 ± 4.3 to 7.4 ± 1.8) during 2001–2002, and by 7.0-fold

(from 26.5 ± 6.3 – 3.8 ± 0.6) during 2002–2003. Graham et al. (1979) and Guerra et al. (1982) also observed that the number of boll weevils captured in traps in the LGRV peaked in September and declined through the onset of spring.

Weather conditions and lack of food are the two main factors that can cause mortality of overwintering boll weevils (Graham et al. 1978, Guerra et al. 1984, Bodden 1997). In the subtropics, boll weevil survival over extended periods is enhanced by mild climatic conditions. In LRGV, the mean monthly air temperature during September–February (2000–2004) ranged from 13.4 to 28.1°C, with a maximum of 19.3–34.6°C and a minimum of 7.4–22.3°C. Several authors have studied the relative cold tolerance of boll weevils (Slosser et al. 1994, Soreson et al. 1996, Suh et al. 2002). More than 90% of nondiapausing weevils tolerated freezing temperatures of 0.0 and –2.5°C for up to 8 h (Slosser et al. 1994). Boll weevil survival during the cotton-free period (overwintering season) may be prolonged by feeding on nonreproductive host plants, which in the overwintering period in the LRGV may include pollen and leaves of cultivated and weedy plants, but these sources are less preferred and are suboptimal for survival (Jones 1997). Summy et al. (1993) and Bodden (1997) related the reduction in numbers of trapped weevils over the overwintering period with their mortality and attributed the absence of cotton fruit as the main factor. Summy et al. (1993) noted that certain species of the genera *Cienfuegosia*, *Sphaeralcea*, *Thespesia*, and *Hibiscus* can serve as reproductive hosts of boll weevils. However, weevils deprived of cotton as a food source are unable to overwinter successfully in warm regions (Fye et al. 1970, Guerra et al. 1984, Summy et al. 1988).

Overwintering Boll Weevil Feeding and Oviposition Activity. At the onset of the cotton-free period in the LRGV, female boll weevils without access to cotton begin resorbing their unladen eggs and entering reproductive diapause (Summy et al. 1993). However, when provided greenhouse-grown cotton squares on a daily basis in this study, oviposition began after 6.9 ± 0.5 , 14.7 ± 0.6 , and 20.3 ± 0.7 d ($F = 110.1$, $df = 2,27$, $P = 0.001$) of feeding for boll weevils captured in September–October, November–December, and January–February 2002–2003, respectively. Females captured later in the winter fed longer before laying eggs than those captured in the early fall. Thus, our data suggest that it may take longer for females to terminate

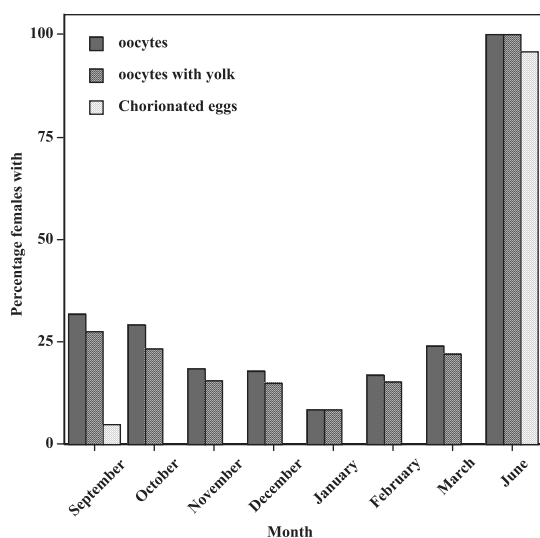


Fig. 1. Mean number of oocytes, oocytes with yolk, and chorionated eggs in ovarioles of boll weevil females captured in pheromone traps at monthly intervals.

diapause the longer they have been dormant. This tendency was observed during three studied seasons (2000–2001, 2001–2002, and 2002–2003). However, the relationship is not clear. Spurgeon and Suh (2003) found that up to 5 wk of starvation after diapause induction did not affect the proportion of females that terminated diapause after switching to a reproductive diet. In our experiments, the rate of feeding by females (Table 1) was significantly less during the winter months of December–February (4.1–5.5 feeding punctures per female per day) than in the fall (9.8–12.4 feeding punctures per female per day in September–November; $F = 15.7$; $df = 5,598$; $P = 0.001$), and this may have affected the rate of diet-mediated termination of dormancy. The nature of the decline in feeding activity over the winter months is an intriguing phenomenon that will require further study. The number of egg punctures per female per day was highest for boll weevils captured in September (9.6 eggs) and lowest in February (0.4 eggs; $F = 52.0$; $df = 5,598$; $P = 0.001$). Similarly, decreases were observed in the ratio of egg punctures to total (eggs + feeding) punctures for weevils captured in September (0.403) to February

Table 2. Survival, development, and sex ratio of boll weevil progeny produced under identical laboratory conditions by females collected in different seasons from the LRGV

Generation of female parent	Percent progeny completing development	Development time of progeny (d)	Percent female progeny
Overwintering	35.0 ± 3.7b	20.2 ± 0.3a	45.6 ± 1.1b
First generation on growing cotton	59.3 ± 1.7a	14.8 ± 0.4b	58.6 ± 2.2a
Second generation on growing cotton	64.4 ± 2.3a	13.9 ± 0.3b	56.6 ± 1.7a

Means ± SE within a column followed by different letters are significantly different (Tukey-Kramer test, $P < 0.05$).

Table 3. Seasonal effects on level of oviposition and duration of window of opportunity (based on longevity) when boll weevils of different generations were provided with cotton squares

Generation	Oviposition (egg punctures)	Window of opportunity for oviposition (d)
Overwintered	38.5 ± 5.6c	25.7 ± 0.8b
First generation on growing cotton	264.6 ± 39.9b	76.2 ± 7.0a
Second generation on growing cotton	385.7 ± 26.2a	70.5 ± 6.5a

Means ± SE within a column followed by different letters are significantly different (Tukey-Kramer test, $P < 0.05$).

(0.079) ($F = 22.2$; $df = 5,598$; $P = 0.001$) and the average percentage of squares that were attacked each day (79.4 in September and 29.0 in February; $F = 46.3$; $df = 5,598$; $P = 0.001$; Table 1).

The number of oocytes in the ovarioles and the number of oocytes containing yolk in boll weevil females were significantly lower during the cotton-free period (September–February) than in the middle of the cotton-growing season (June; $F = 9.2$; $df = 8,237$;

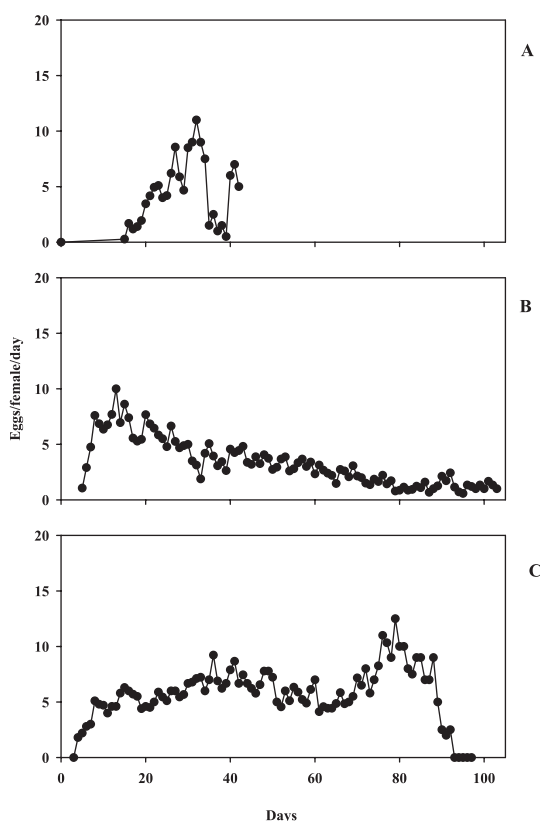


Fig. 2. Lifetime profiles of daily mean oviposition activity of overwintering (A) and first- (B), and second- (C) generation boll weevil females from the LRGV. Overwintering females were captured in pheromone traps, and first and second generations were collected as third instars in cotton squares and reared to adulthood in the laboratory.

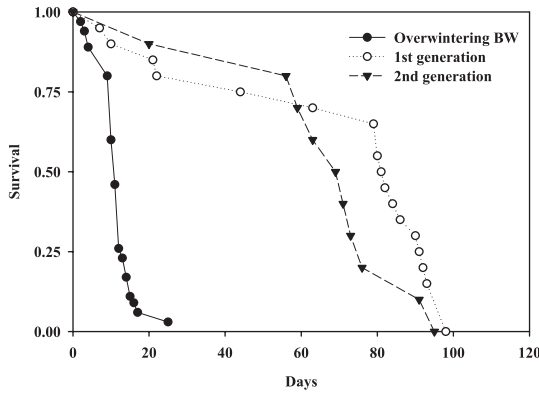


Fig. 3. Survivorship (percentage of live weevils per day from total used in the test) profiles of overwintering and first- and second-generation boll weevil females.

$P = 0.001$ and $F = 10.0$; $df = 8,237$; $P = 0.001$, respectively; Fig. 1). A few females containing chorionated eggs were observed in September (4.8%). In June, 96% of the sampled females contained chorionated eggs. These characteristics are consistent with the boll weevils captured in the cotton-free period entering or being in diapause and those captured in June being in a reproductive state (Spurgeon et al. 2003).

Development and Reproduction of Overwintering, First-, and Second-Generation Boll Weevils. To estimate the dynamics of boll weevil populations, it is important to understand changes in development and reproduction of the insect during the cotton-free period relative to the first and second generations in the growing season. The percentage of progeny that developed to adulthood under identical laboratory conditions differed among female parents collected from overwintering and first and second generations ($F = 25.7$; $df = 2,48$; $P = 0.001$). First- and second-generation females produced a significantly higher percentage of eggs yielding adult progeny (59.0% and 64.4%) than did overwintering weevils (35.0%; Table 2). We also observed seasonal effects on the proportion of progeny that were females ($F = 19.5$; $df = 2,48$; $P = 0.001$), with females of the first and second generations producing a higher percentage of female progeny than overwintering females (56.6 and 58.6 versus 45.6%). Development time of offspring from overwintering female parents was significantly longer than those from first- and second-generation parents ($F = 79.3$; $df = 2,57$; $P = 0.001$; Table 2).

The duration of the window of opportunity for oviposition when provided with cotton squares was

greater for females of the first (76.2 d) and second generations (70.5 d) of the growing season than for overwintered weevils (25.7 d) ($F = 71.6$; $df = 2,62$; $P = 0.001$; Table 3). Seasonal effects also were observed on the oviposition ($F = 33.1$; $df = 2,62$; $P = 0.001$; Table 3). The total number of egg punctures produced by females of the second generation from growing cotton were ≈ 10.02 -fold higher than for overwintering females (385.7 versus 38.5), and 1.5-fold higher than for first-generation females (385.7 versus 264.6). The percentage of days on which females oviposited during their lifetime increased in the first and second generations ($F = 12.9$; $df = 2,57$; $P = 0.001$). On average, overwintering females oviposited on $53.4 \pm 4.0\%$ days of their lifetime, whereas females of the first and second generations oviposited on 75.3 ± 3.0 and $87.1 \pm 3.5\%$ days of their adulthood, respectively. The comparison of seasonal fluctuations in oviposition are relevant to calculating population growth, because the parameters measured for the overwintering females represent reproductive potential after emerging from diapause.

Oviposition was significantly influenced by both time (days after capture [overwintering] or after eclosion from pupa [first and second generations]) ($P < 0.001$) and season ($P < 0.001$). In addition, the time by season interaction was significant ($P < 0.001$), indicating that the temporal pattern of oviposition activity differed among overwintering and first- and second-generation females. For overwintering females, oviposition did not begin until day 15 after the conditioning period, a pattern expected of females terminating diapause after collection. After onset of oviposition, the average number of oviposition punctures slowly increased to a peak of ≈ 9 –11 eggs per day by 31–34 d after capture, followed by a rapid decline. Overwintering females laid eggs beyond day 43 (Fig. 2a). A similar pattern of oviposition was observed for first-generation females (Fig. 2b), except the durations of the peak and decline were greatly lengthened, and total egg production was higher compared with the overwintering females. The last egg laid by first-generation females was on day 103. For second-generation females, oviposition began at day 3 after the conditioning period, the total egg production was generally higher than for overwintering and first-generation females, and peak of oviposition was late and ≈ 10 d in duration, followed by a sharp decline at about day 90 (Fig. 2c).

Survivorship of female weevils (percentage of weevils remaining alive each day) varied significantly among the seasons ($\chi^2 = 57.6$; $df = 2$; $P = 0.001$; Fig.

Table 4. Life table statistics for progeny of boll weevil females by generation (values in parentheses are 95% confidence intervals)

Generation	R_0	r_m	λ	T	DT
Overwintering	6.2 (4.4–8.0)	0.09 (0.08–0.11)	1.09 (1.08–1.11)	19.7 (18.1–21.3)	7.4 (6.4–8.5)
First generation	91.9 (62.9–120.9)	0.16 (0.12–0.19)	1.17 (1.13–1.21)	28.2 (23.3–33.2)	4.3 (3.4–5.3)
Second generation	139.9 (76.2–203.5)	0.14 (0.11–0.17)	1.15 (1.12–1.18)	35.1 (27.9–42.3)	4.9 (4.0–5.8)

R_0 , net reproductive rate; r_m , intrinsic rate of increase; λ , finite rate of increase; T, mean period over which progeny are produced (d); DT, doubling time of the population (d).

3). The pairwise comparisons revealed the survivorship of overwintering females was lower than first-generation ($\chi^2 = 38.5$, $df = 2$, $P = 0.001$) and second-generation ($\chi^2 = 29.1$; $df = 2$; $P = 0.001$) females. Females of first and second generations had comparable survivorships ($\chi^2 = 2.08$; $df = 2$; $P = 0.15$).

The values of life table statistics calculated for boll weevil females differed among seasons (Table 4). First- and second-generation boll weevils were predicted to increase at significantly higher mean constant exponential rates (r_m) than the overwintering generation. Life table calculations indicated that the second generation boll weevil populations increased an average 1.5-fold higher each generation (R_o) than females at first-generation populations and 22.6-fold higher than for overwintering populations. Growth rate and progeny production of overwintering populations were 2.3-fold less than for first-generation populations and 2.7-fold less than for second-generation populations.

Discussion

Knipling (1960a,b) theoretically predicted range of boll weevil population values and estimated populations increase at those possible levels from low values of 2.5-fold in unfavorable overwintering period to 5-fold as a moderate increase, and to 7.5-fold as a high increase in favorable cotton-growing period. Lloyd et al. (1964) found the average rate of increase of boll weevil populations was close to five-fold per generation. Lloyd and Merkl (1961) suggested that the rate of oviposition is related to the density of the population. Dunnam (1929) showed that an average of 67 overwintering boll weevils per acre punctured <5% of the squares, whereas the first- and second-generation populations descended from those overwintering weevils had increased to 2,000 per acre, with punctured square infestations of 60%. Sanderson (1904) observed that the number of boll weevils in the first generation was ≈ 15 times greater than the overwintering population. The average life of overwintering boll weevils after emergence from diapause was 20–22 d, but first-generation weevils lived an average 41.5 d (Fye et al. 1959). In an isolated plot, Walker (1962) reported that, during 1960, the total emerging F_1 generation (13,354 weevils) represented an increase of about five-fold over the average overwintered weevil infestation (2,693 weevils). In 1961, the F_1 (6,050 weevils) increase over the parent population (2,728 weevils) was only two-fold (Walker 1962). Bailey et al. (1972) also showed a variation in oviposition between overwintering boll weevils, first, and second generations when adult boll weevils fed on standard diet and maintained at constant laboratory conditions.

Knowledge of the rate of increase of a population from one generation to the next is basic to an understanding of the degree of control that is needed to hold insects to no economic levels. Our data showed seasonal variation in boll weevil survival, development, and reproductive potential between the overwintering and first and second generations of boll weevil

females when maintained under similar controlled conditions in the laboratory. This trend was observed during four seasons from 2002 to 2005 and suggests that boll weevils may have inherent seasonal variations in these parameters.

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References Cited

- Bailey, J. C., F. G. Maxwell, and J. N. Jenkins. 1972. Seasonal fluctuations in oviposition of the boll weevil in the laboratory. *J. Kansas Entomol. Soc.* 45: 252–254.
- Bodden, E. A. 1997. The spread and establishment of the cotton boll weevil in the Texas High Plains. MS thesis. Texas Tech. Univ., Lubbock, TX.
- Dunnam, E. W. 1929. Experiments on the relation between location of cotton fields and the intensity of boll weevil infestation the succeeding season. *J. Econ. Entomol.* 21: 750–756.
- Everett, T. R., and J. O. Ray. 1962. The utility of sealed punctures for studying fecundity and egg laying by the boll weevil. *J. Econ. Entomol.* 55: 651–656.
- Everett, T. R., and N. W. Earle. 1964. Boll weevil oviposition responses in cotton squares and various other substrates. *J. Econ. Entomol.* 57: 651–656.
- Fye, R. E., W. W. McMillian, A. R. Hopkins, and R. L. Walker. 1959. Longevity of overwintered and first generation boll weevils at Florence, South Carolina. *J. Econ. Entomol.* 52: 453–454.
- Fye, R. E., J. E. Leggett, and C. D. Bonham. 1970. Winter survival of the boll weevil complex in Arizona. *J. Econ. Entomol.* 63: 1071–1074.
- Graham, H. M., N. S. Hernandez, J. R. Llanes, and J. Tamayo. 1978. Overwintering habitats of the boll weevil in the Lower Rio Grande Valley of Texas. *Environ. Entomol.* 7: 345–348.
- Graham, H. M., N. S. Hernandez, J. R. Llanes, and J. Tamayo. 1979. Seasonal incidence of diapause in boll weevil populations in the Lower Rio Grande Valley of Texas. *Southwest. Entomol.* 4: 170–175.
- Greenberg, S. M., T. W. Sappington, D. W. Spurgeon, and M. Setamou. 2003. Boll weevil (Coleoptera: Curculionidae) feeding and reproduction as functions of cotton square availability. *Environ. Entomol.* 32: 698–704.
- Greenberg, S. M., T. W. Sappington, M. Setamou, and R. J. Coleman. 2004. Influence of different cotton fruit sizes on boll weevil (Coleoptera: Curculionidae) oviposition and survival to adulthood. *Environ. Entomol.* 33: 443–449.
- Greenberg, S. M., D. W. Spurgeon, T. W. Sappington, and M. Setamou. 2005. Size-dependent feeding and reproduction by boll weevil (Coleoptera: Curculionidae). *J. Econ. Entomol.* 98: 749–756.
- Guerra, A. A., R. D. Garcia, and J. A. Tamayo. 1982. Physiological activity of the boll weevil during the fall and winter in subtropical areas of the Rio Grande Valley of Texas. *J. Econ. Entomol.* 75: 11–15.
- Guerra, A. A., R. D. Garcia, P. R. Bodegas, and M. E. DeCoss. 1984. The quiescent physiological status of boll weevils (Coleoptera: Curculionidae) during the noncotton season in the tropical zone of Soconusco in Chiapas, Mexico. *J. Econ. Entomol.* 77: 595–598.

- Hommel, G. 1988. A stage wise rejective multiple test procedure based on a modified Bonferroni test. *Biometrics* 75: 383–386.
- Hulting, F. L., B. Orr, and J. J. Obrycki. 1990. A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life table parameters. *Fla. Entomol.* 73: 601–612.
- Jones, R. W. 1997. Pollen feeding by the boll weevil (Coleoptera: Curculionidae) following cotton harvest in East Central Texas. *Southwest. Entomol.* 22: 419–429.
- Knipling, E. F. 1960a. Requirements and possibilities of boll weevil control and eradication in relation to the population dynamics of the insect. p. 11. *Ann. Cotton Insect Control Conference*, 14–15 January 1960, Memphis, TN.
- Knipling, E. F. 1960b. Use of insects for their own destruction. *J. Econ. Entomol.* 53: 415–420.
- Littell, R. C., G. A. Milliken, W. W. Stoup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, NC.
- Lloyd, E. P., and M. E. Merkl. 1961. Seasonal occurrence of diapause in the boll weevil in Mississippi. *J. Econ. Entomol.* 54: 1214–1216.
- Lloyd, E. P., M. L. Laster, and M. E. Merkl. 1964. A field study of diapause, diapause control, and population dynamics of the boll weevil. *J. Econ. Entomol.* 57: 433–436.
- Sanderson, E. D. 1904. The cotton boll weevil in Texas. *Farmer's Bulletin* (United States Dep. of Agriculture), Washington, DC.
- Sappington, T. W., and D. W. Spurgeon. 2000. Preferred technique for adult sex determination of the boll weevil (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 93: 610–615.
- SAS Institute. 1999. SAS/STAT user's guide, version 8. SAS Institute, Cary, NC.
- Setamou, M., F. Schulthess, N. A. Bosque-Perez, H. M. Poehling, and C. C. Borgemeister. 1999. Bionomics of *Mussidia nigricornella* (Lepidoptera: Pyralidae) on three host plants. *Bull. Entomol. Res.* 89: 465–471.
- Slosser, J. E., R. Montandon, D. R. Rummel, T. W. Fuchs, and L. T. Wilson. 1994. A cold bath technique for determining diapause status of the boll weevil, pp. 990–991. *In* P. Dugger and R. Ritcher (eds). *Proceedings of the Beltwide Cotton Conference*. National Cotton Council, Memphis, TN.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry. The principles and practice of statistics in biological research*, 3rd ed. W. H. Freeman and Co., New York.
- Soreson, C. E., R. D. Parker, and M. B. Layton. 1996. Relative cold tolerance of boll weevil from Missouri, Mississippi, and coastal Texas, pp. 716–717. *In* P. Dugger and R. Ritcher (eds.). *Proceedings of the Beltwide Cotton Conference*. National Cotton Council, Memphis, TN.
- Spurgeon, D. W., and C. P.-C. Suh. 2003. Diet-mediated termination of boll weevil dormancy, pp. 1511–1514. *In* P. Dugger and R. Ritcher (eds.). *Proceedings of the Beltwide Cotton Conference*. National Cotton Council, Memphis, TN.
- Spurgeon, D. W., T. W. Sappington, and C. P.-C. Suh. 2003. A system for characterizing reproductive and diapause morphology in the boll weevil (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 96: 1–11.
- Suh, C. P.-C., D. W. Spurgeon, and J. K. Westbrook. 2002. Influence of feeding status and physiological condition on supercooling points of adult boll weevils (Coleoptera: Curculionidae). *Environ. Entomol.* 31: 754–758.
- Summy, K. R., J. R. Cate, and W. G. Hart. 1988. Overwintering strategies of boll weevil in southern Texas: reproduction and cultivated cotton. *Southwest. Entomol.* 13: 159–164.
- Summy, K. R., J. R. Cate, and D. Bar. 1993. Overwinter survival of boll weevil (Coleoptera: Curculionidae) in Southern Texas: evidence and significance of reproductive diapause. *J. Econ. Entomol.* 86: 369–375.
- Walker, J. K., Jr. 1962. Emergence pattern of first generation boll weevils in an isolated plot during 1960 and 1961. *J. Econ. Entomol.* 55: 795–796.
- Wolfenbarger, D. A., H. M. Graham, R. D. Parker, and J. W. Davis. 1976. Seasonal patterns of boll weevil response to traps baited with grandlure in the Lower Rio Grande Valley. *Tex. Agric. Exp. Stn. Res. Monogr.* 8: 20–25.

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